A REDESCRIPTION OF THE ANOMALOCYSTITID MITRATE *RHENOCYSTIS LATIPEDUNCULATA* FROM THE LOWER DEVONIAN OF GERMANY

by M. RUTA *and* C. BARTELS

ABSTRACT. The anomalocystitid mitrate *Rhenocystis latipedunculata*, from the Lower Devonian Hunsrückschiefer of Rhineland, Germany, is reconstructed and redescribed. *Rhenocystis* is characterized by transverse, terrace-like ridges on two antero-posteriorly elongate, postero-lateral areas of the dorsal head skeleton and on the posterior third of the ventral head skeleton; the relatively small size of the ventral plates of the second transverse row; a suture between the mid-ventral plates of the first and third row; the relatively large size of the placocystid plate; the presence of rocking articulations between dorsal and ventral fore tail plates; a transversely expanded and recumbent anterior styloid blade; a robust, spike-like posterior blade; and four morphologically distinct regions in the hind tail. *Rhenocystis* closely resembles *Placocystites forbesianus* from the middle Silurian of England and *Victoriacystis wilkinsi* from the upper Silurian of Australia, with which if forms a clade within the anomalocystitids of boreal type.

IN this paper, we reconstruct and redescribe the Lower Devonian anomalocystitid mitrate *Rhenocystis latipedunculata* Dehm, 1932 from the Hunsrückschiefer of the Rhineland, Germany, and discuss its affinities. *Rhenocystis* is one of the most abundant boreal anomalocystitids known to date. Intense collecting activity during the last 20 years has yielded several new specimens which provide additional morphological information. The recently collected material comes from the Eschenbach-Bocksberg roof-slate quarry near the village of Bundenbach, Germany (Text-fig. 1A). As with other Hunsrückschiefer fossils, it is difficult to establish the precise levels in which the specimens were found, as these were collected from 'hills' of waste slabs (Bartels and Brassel 1990). A privately owned specimen found near Gemünden (Dehm 1934) represents the only record of *Rhenocystis* outside the Bundenbach area. In the present work, the plate nomenclature is based on a revised terminology of the anomalocystitid skeleton which will be discussed by one of us (MR) elsewhere. This paper is dedicated to Professor Richard Dehm for his contribution to the knowledge of the anomalocystitid mitrates.

Repositories. BMNH, The Natural History Museum, London, UK; BSPHG, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; DBM-HS, Deutsches Bergbau-Museum, Bochum, Germany.

GEOLOGICAL SETTING

Lithology, palaeoenvironment and age. A recent, comprehensive summary of the geology and stratigraphy of the Hunsrückschiefer (or Hunsrück Slate) is found in Bartels and Brassel (1990). The fossils are preserved in dark grey slates of mid Early Emsian age (Krebs 1979; Briggs *et al.* 1996). The presence of euhedral crystals of chlorite and muscovite formed *in situ* indicates that the sediment was subject to metamorphism at relatively low temperature and high pressure (anchizone; see Briggs *et al.* 1996). Cleavage lies at various angles with respect to the bedding planes, and is commonly visible on the surface of the fossils.

There is no general consensus as to the depth of water at which the sediment was deposited;

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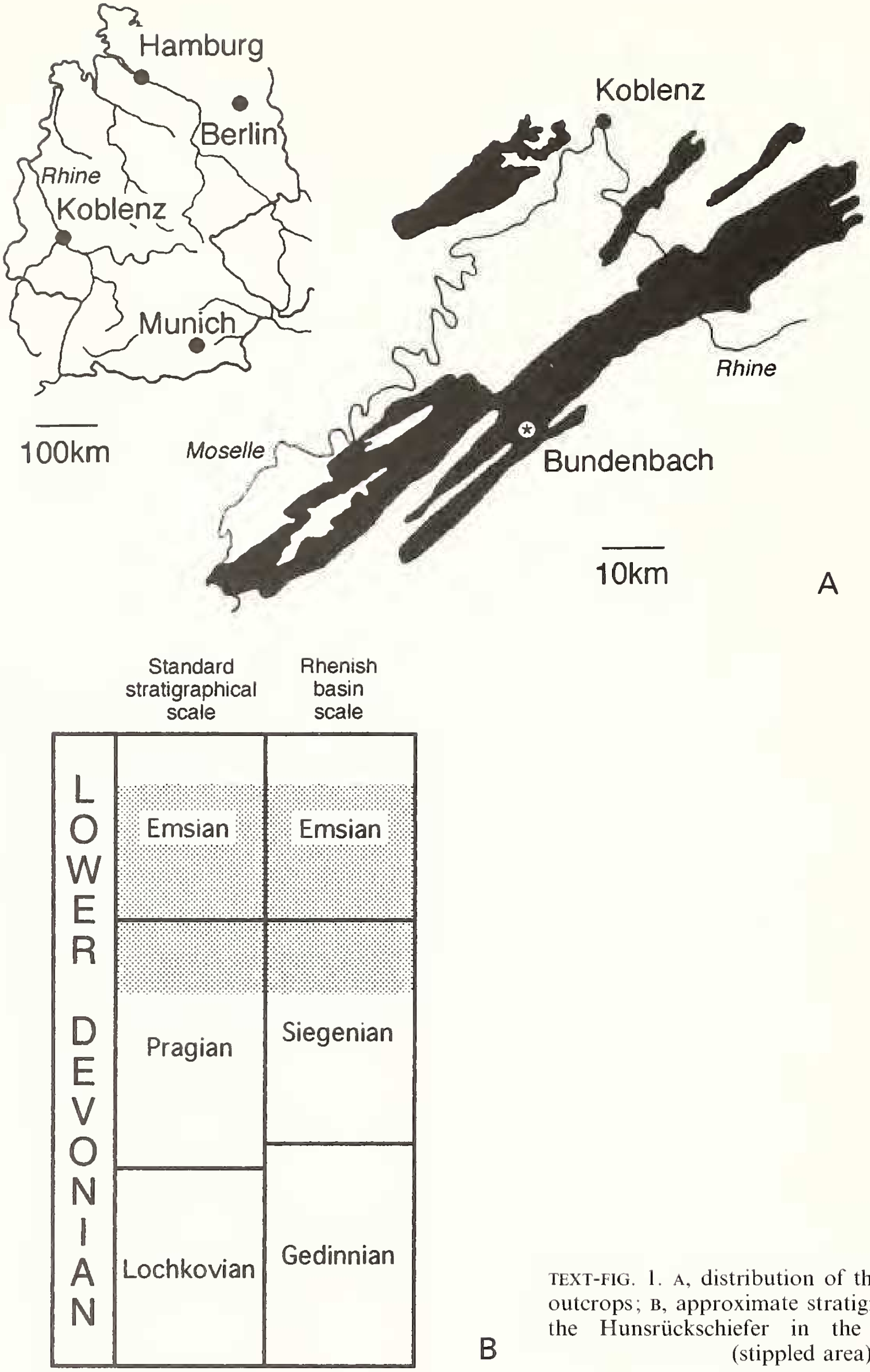


TEXT-FIG. 1. A, distribution of the Hunsrückschiefer outcrops; B, approximate stratigraphical position of the Hunsrückschiefer in the Lower Devonian (stippled area).

although variable in different parts of the basin, the maximum depth was probably not much greater than 200 m (Briggs *et al.* 1996; see also Stürmer and Bergström 1973; Krebs 1979, and references therein). The basin became shallower both in a north-westerly and in a south-easterly direction. The Hunsrück Slate deposits represent an intra-shelf basin within the Rhenohercynian basinal province. The nature of the lithofacies, the presence of distal turbidites (which explains in part the sandy intercalations) often preserving assumed allochthonous fossils, the fact that most of the autochthonous echinoderms possess thin skeletons (presumably suggesting a relatively deep water environment), the presence of few solitary corals, the absence of stromatoporoids, and the preponderance of nektic and planktic organisms among the non-echinoderm taxa show that the Hunsrück Slate facies can be assigned to the Hercynian magnafacies. According to Krebs (1979), such a facies possibly reflects an open marine environment.

According to more recent interpretations (O. Sutcliffe, pers. comm. to MR 1997), the palaeoenvironment of the typical Hunsrück Slate fossils probably corresponds to the interchannel areas of a submarine fan. A muddy substrate benthic community lived in oxygenated waters above the level of the storm wave base and was occasionally buried by sediment transported by density currents caused by sudden influxes of mud (Stürmer and Bergström 1973; Bartels and Brassel 1990; Briggs *et al.* 1996).

In the Rhenish basin stratigraphical scale of Germany (Text-fig. 1B), the lithologies of the Hunsrück Slate are assigned either to the lowermost Emsian (or Ulmen substage) (Hunsrück Slate *sensu stricto*) or to the interval between the uppermost Siegenian (Heredorf substage) and the middle Lower Emsian (Singhofen substage) (Hunsrück Slate *sensu lato*). The Bundenbach rocks are generally attributed to the uppermost Ulmen substage; as such, they are part of the Hunsrück Slate *sensu stricto*. However, recent study of the lithology of the Hunsrück Slate (O. Sutcliffe, pers. comm. to MR 1997) reveals that the Bundenbach rocks should be assigned to the Singhofen substage, based on the presence of volcanic tuffs. Therefore, the Bundenbach slates should be regarded as middle Lower Emsian following the Rhenish stratigraphical subdivisions.

A more precise correlation with other Early Devonian rocks is possible on the basis of Hercynian faunal elements. The presence of dacryoconarids (Alberti 1982) and of representatives of the *Anetoceras* goniatite fauna (Chlupač 1976) indicates that the Bundenbach rocks are probably mid Zlichonian in age (*praecursor* dacryoconarid Zone), and hence well above the uppermost Pragian.

Taphonomy and diagenesis. The presence of well preserved articulated fossils in the Hunsrückschiefer indicates that the organisms were buried rapidly and that transport was either absent or occurred over short distances. Fossils belonging to different phyla are often closely associated on the same slab or even overlap each other. These associations are sometimes regarded as accumulations of dead organisms in shallow areas of the sea floor, which were relatively protected from the action of bottom currents; interruption of transport caused by obstacles is also often invoked to explain such accumulations. There are indications that some heterogeneous associations reflect, in part, life associations, and that organisms lying close to each other were probably engaged in a particular biological activity (e.g. exploitation of the same localized food source) before being killed by burial. Many of the crinoids are found rooted in place and merely smothered by turbidity currents. Several vagile organisms left tracks before dying (e.g. Richter 1941; Seilacher and Hemleben 1966; Bartels and Brassel 1990). The analysis of trace fossils (O. Sutcliffe, pers. comm. to MR 1997) indicates that many organisms were alive before, during and after the mud influx episodes.

The vast majority of specimens of *Rhenocystis* are virtually complete. Disruption of the skeletal plates is rare and affects mainly the head. The flexibly articulated upper lip plates, for example, are often found displaced, and the same is true for the lateral elements of the anteriormost transverse row of ventral plates. Conversely, the mid-ventral placocystid plate (Caster 1952), or plate V17 (see below), is often articulated with the rest of the skeleton; this condition occurs rarely in other anomalocystitid mitrates (Derstler and Price 1975; Jefferies and Lewis 1978; Ubaghs 1979; Craske and Jefferies 1989; Parsley 1991; Ruta 1997). The spines are usually in place, or only slightly displaced. The tail is often complete.

Exceptional preservation of soft tissues in Hunsrückschiefer fossils, with authigenic pyrite replacing organic matter, has been documented in some echinoderms and arthropods (Stürmer *et al.* 1980; Bartels and Brassel 1990), and has been studied in detail by Briggs *et al.* (1996). Unfortunately, soft tissue preservation has not been documented in *Rhenocystis*, owing to extensive pyritization. In many specimens, mass concentration of small to medium-sized euhedral crystals of pyrite, with large euhedral crystals often interspersed throughout, line the edges of the articulated spines, the sutures between adjacent skeletal head plates as well as the lumens of broken tails. Concentrations of large crystals are probably the effect of localized phenomena of supersaturation (Murowchick and Barnes 1987; Briggs *et al.* 1996). Aggregations of subhedral to large euhedral crystals, the latter sometimes found isolated and formed presumably during later stages of diagenesis (Briggs *et al.* 1996), are visible on the external surface of the articulations between dorsal and ventral fore tail plates, on the styloid blades, across the sutures between adjacent hind tail segments, and along the external margins of the hind tail ossicles and plates. Such aggregations form irregular patches or lumps of different shapes and sizes. Often, the pyrite replacing the calcitic skeleton has a fine texture.

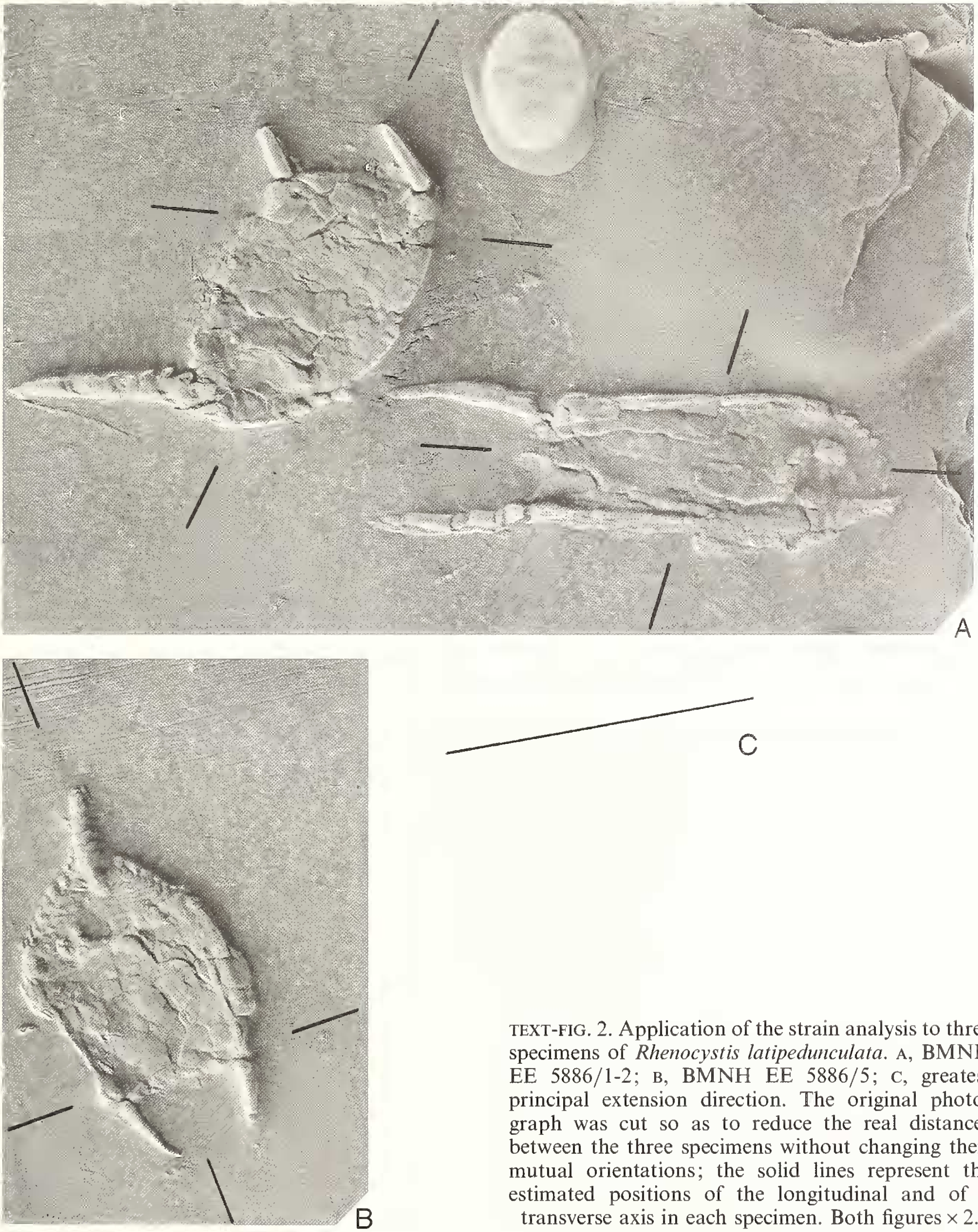
METHODS

The vast majority of the specimens was prepared using an air-abrasive machine and fine iron powder as an abrasive. This technique leads to spectacular results (see Bartels and Brassel 1990), leaving the fossils virtually untouched and fully exposed. The specimens were wetted with water or, in the case of extensive pyritization, sprayed with ammonium chloride before being photographed. The best photographic results were obtained using a low angle of illumination, which allows plate sutures to be distinguished from penetrative cleavage (see also Dehm 1932, 1934).

Most Hunsrückschiefer fossils are deformed to various degrees by tectonic strain. Ramsay and Huber (1983) provided a detailed account of tectonic strain analysis. The application, advantages and limitations of such analysis to deformed fossils have been discussed by Wellman (1962), Cooper (1990), Fortey and Owens (1992), Hughes and Jell (1992) and Rushton and Smith (1993) among others. Almost undeformed, dorso-ventrally compressed individuals of *Rhenocystis* indicate that, like the vast majority of the anomalocystitids, this mitrate was externally bilaterally symmetrical in life. It is, therefore, possible to identify, with some approximation, the positions of the longitudinal and a transverse axis. These would be orthogonal in undeformed specimens. The restoration involves the construction of a strain ellipse starting from deformed right angles, under the assumptions that the deformation occurred homogeneously in the planes of bedding, that the specimens lay flat on or within such planes, and that their dorso-ventral flattening, due to compaction and loss of water, did not modify their original shape and size (Cooper 1990; Rushton and Smith 1993).

The available methods of fossil retrodeformation using deformed right angles require either two specimens or one specimen and the direction of mineral elongation (Cooper 1990). Stürmer *et al.* (1980) and Jefferies (1984) published X-ray photographs of a slab with *c.* 17 individuals of *Rhenocystis* lying close to each other and at different depths with respect to the two main surfaces of the slab. A cast of the slab was made available for study. Of the *c.* 17 individuals of *Rhenocystis*, eight are exposed in dorsal view. Specimens BMNH EE 5886/1–2 and 5 were chosen for the strain analysis and photographed. For each specimen, the positions of the longitudinal and a transverse axis were estimated. The axes are indicated by black bars drawn directly on the photograph (Text-fig. 2A–B). The determination of the position of the two axes, like all the subsequent steps of the retrodeformation process, is subject to error. The most obvious source of error occurs because individuals show a certain amount of disruption, albeit small. Each of the above-mentioned assumptions underlying the application of strain analysis constitutes an additional source of error.

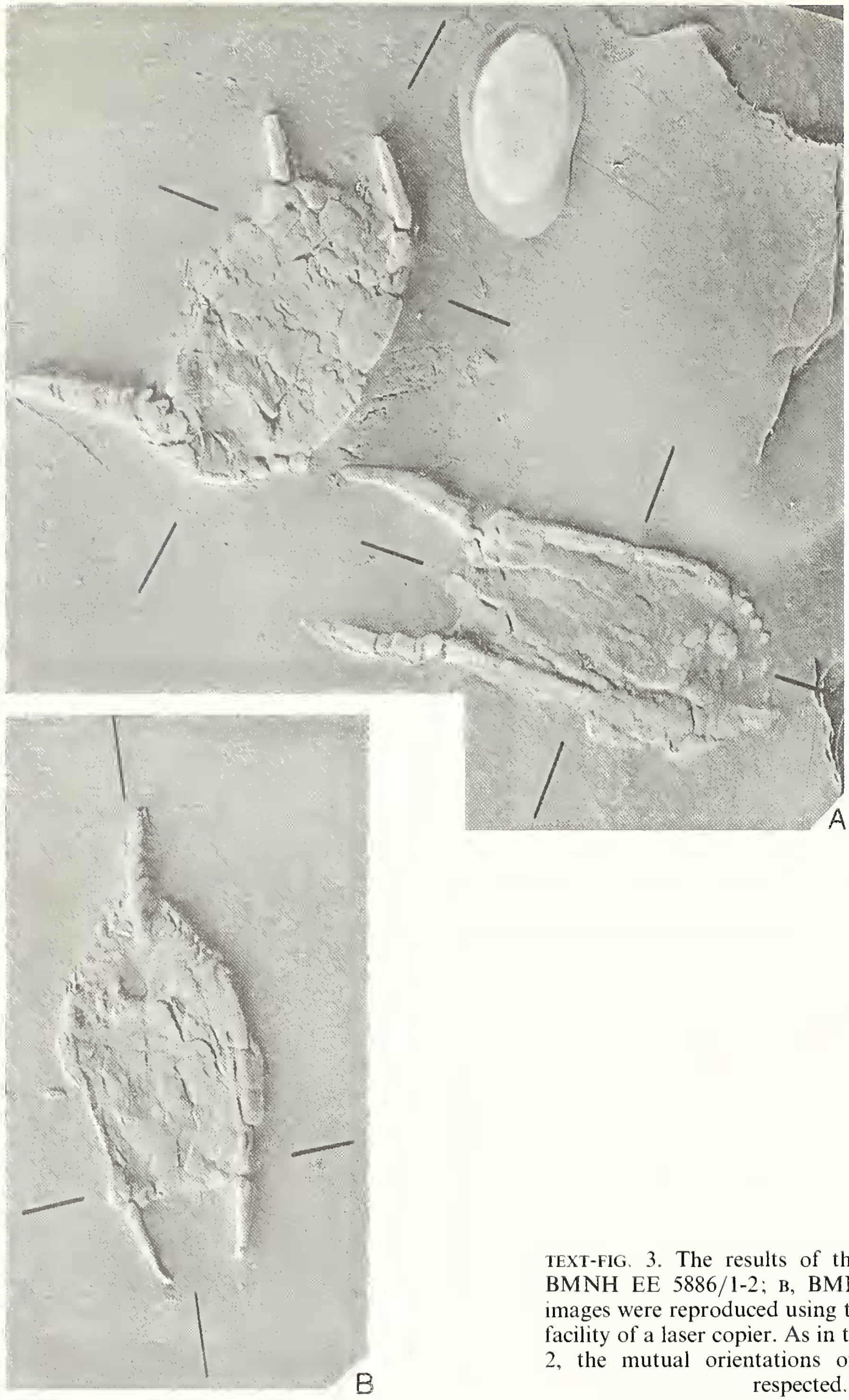
Of the various techniques available to correct for tectonic distortion of fossils (see review in Cooper 1990), we chose Breddin curves, a graphical method used to calculate the strain ratio from the values of angular shear strain (deviation from the right angle) and angular orientation of the



TEXT-FIG. 2. Application of the strain analysis to three specimens of *Rhenocystis latipedunculata*. A, BMNH EE 5886/1-2; B, BMNH EE 5886/5; C, greatest principal extension direction. The original photograph was cut so as to reduce the real distances between the three specimens without changing their mutual orientations; the solid lines represent the estimated positions of the longitudinal and of a transverse axis in each specimen. Both figures × 2.

fossils with respect to the axes of the strain ellipse (Ramsay and Huber 1983). A set of curves allows the strain ratio and the direction of the axes of the strain ellipse to be determined approximately.

The Breddin curves method gave a strain ratio value of *c*. 1·37. On the basis of this value, it was



TEXT-FIG. 3. The results of the strain analysis; A, BMNH EE 5886/1-2; B, BMNH EE 5886/5. The images were reproduced using the anamorphic zoom facility of a laser copier. As in the case of Text-figure 2, the mutual orientations of the specimens are respected.

possible to retrodeform the three specimens of *Rhenocystis* using the simple technique outlined by Rushton and Smith (1993). The directions of the two axes of the strain ellipse were drawn on the original photograph before the latter was cut into two parts for publication (Text-fig. 2A–B). The original photograph was photocopied (Text-fig. 3) applying the 'anamorphic zoom' facility of a laser copier, which enables the operator to change the relative lengths of two orthogonal axes once the greatest principal extension direction (long axis of the strain ellipse; Text-fig. 2C) is known.

The laser copy image shows that the relative proportions of BMNH EE 5886/1–2 and 5 are approximately the same, although in none of the three corrected specimens is the longitudinal axis accurately perpendicular to the transverse axis, by reason of the amount of error introduced during the retrodeformation process. The approximate values of the angles between these axes (clockwise measurements are positive) are 87° in BMNH EE 5886/1 (Text-fig. 3A), 93° in BMNH EE 5886/2 (Text-fig. 3A), and 86° in BMNH EE 5886/5 (Text-fig. 3B). The results of the retrodeformation process are to be considered only as a crude estimate of the original external morphology of the fossils.

SYSTEMATIC PALAEONTOLOGY

Superphylum DEUTEROSTOMIA Grobben, 1908
(Stem group of the Craniata?)

Genus RHENOCYSTIS Dehm, 1932

Type species. Rhenocystis latipedunculata Dehm, 1932 by monotypy.

Rhenocystis latipedunculata Dehm, 1932

Plates 1–10; Text-figures 2–6

1932 *Rhenocystis latipedunculata* Dehm, p. 66, figs 1–6; pl. 2, figs 1–4.
1934 *Rhenocystis latipedunculata* Dehm; Dehm, p. 24, fig. 2a–e; pl. 1, figs 4–9; pl. 2, figs 1–2.
1952 *Rhenocystis* Dehm 1933 [*sic*]; Caster, p. 19, fig. 2i–j.
1960 *Rhenocystis* Dehm 1933 [*sic*]; Gill and Caster, p. 45.
1961 *Rhenocystis latipedunculata* Dehm; Kuhn, p. 12, figs 13, 1–4, 14.
1968 *Rhenocystis latipedunculata* Dehm; Ubaghs, p. 560, figs 332, *6*, 359, *1a–b*.
1970 *Rhenocystis latipedunculata* Dehm; Kutscher, p. 96.
1975 *Rhenocystis latipedunculata* Dehm; Kutscher, p. 48, fig. 5a–e.
1987 *Rhenocystis* Dehm; Regnault and Chauvel, p. 672.
1989 *Rhenocystis* Dehm 1933 [*sic*]; Craske and Jefferies, p. 95.
1990 *Rhenocystis latipedunculata* Dehm; Bartels and Brassel, p. 175, fig. 161.
1990 *Rhenocystis latepedunculata* [*sic*]; Cripps, p. 59.
1991 *Rhenocystis* Dehm; Parsley, p. 13.
1991 *Rhenocystis latipedunculata*; Südkamp, p. 239.

Holotype. BSPHG 1928 VII 2.

Type locality, type horizon and age. Bundenbach, Rhenish Massif, Germany; *praecursor* dacryoconarid Zone; 'Hans' sequence; Upper Pragian to Lower Emsian.

Additional material. BMNH E 23605, 23660, 29315–29316, EE 5647, 5886 (P31), 5887 (Brassel SNG 108), 5888 (Brassel SNG 110), 5889 (Brassel SNG 111), 5890 (Brassel SNG 112), 5891 (Brassel SNG 114), 5892 (Brassel SNG 116), 5893 (Brassel SNG 117), 5894 (XXI 22a), 5895 (XXI 22b), 5898 (BSPHG 1928 VII 1), 5899 (BSPHG 1928 VII 2), 5900 (BSPHG 1930 III 17), 5901 (BSPHG 1931 I 48), 5902 (BSPHG 1931 I 49); DBM-HS 295–302, 347, 472, 524, 564, 566–567, 570, 727, 743–745, 750. WB 514.

WB 514 is a provisional registration number for a specimen in the Deutsches Bergbau-Museum, Bochum. Labels in parentheses for BMNH EE 5886–5895 refer to originals in the Senckenberg Museum, Frankfurt, whereas those for BMNH EE 5898–5902 refer to originals in the Staatssammlung, Munich.

The Bergbau-Museum material comes from the Eschenbach-Bocksberg quarry near Bundenbach (approximate coordinates: 07°27′ E; 49°51′ N), but precise data concerning the localities where the other specimens were found are not known.

Diagnosis. Anomalocysitid mitrate with five transverse rows of ventral plates; in antero-posterior succession, such rows consist of five, four, three, five and three elements respectively; V1 and V5 comparatively small with respect to the other elements of the first row; V6–V9 subequal in size and much smaller than V2–V4; V3 and V12 in contact with each other, thus interrupting the second transverse row; V17 rounded and comparable in size to V16 and V18; sutures between V15 and V16, and between V18 and V19, medially convex; V21 shield-shaped and deeply inserted between V20 and V22, but not separating these two plates completely; posterior part of the lateral margins of V20 and V22 slightly turned laterally; presence of two centro-dorsal plates A and C; flexible articulation formed by plates MOP and right and left LOP against plates DLM, A and C; spines slightly convex externally in dorsal aspect and with a blunt median and a sharp lateral edge; ventral sculpture consisting of robust, transversely elongate, terrace-like ridges mainly confined to plates V20–V22; posterior ventral ridges more irregular than anterior ventral ridges; dorsal sculpture consisting of ridges mainly confined to plates PLM; lateral head walls well-developed and sloping slightly ventralward and lateralward; fore tail much wider anteriorly than posteriorly, and with dorsal plates smaller than the ventral plates; rocking articulations between dorsal and ventral fore tail plates; styloid with dorsal keel, a transversely expanded, recumbent anterior blade, and a robust, spike-like posterior blade; the latter is triangular in cross section and bears a flat, transverse posterior surface; first hind tail ossicle robust and comparable in size and shape to the posterior styloid blade; successive proximal ossicles decreasing rapidly in size; ossicle shape changing remarkably throughout the length of the tail; most ventral hind tail plates with a lateral knob; proximal hind tail plates with a longitudinal keel near their dorsal margin.

DESCRIPTION AND FUNCTIONAL MORPHOLOGY

Variation: how many species of Rhenocystis?

The application of strain analysis (see above) demonstrates that estimates of body proportions in deformed fossils by visual inspection are highly misleading (Cooper 1990; Rushton and Smith 1993). Several examples from the Hunsrück Slate show that the shapes of individuals of the same species occurring on the same slab or found at a considerable distance from one another can be dramatically affected by distortion. Individual, ontogenetic, sexual or specific variations in *Rhenocystis* cannot be discerned on the basis of the available evidence. As Dehm (1934) pointed out, part of the observed variation in *Rhenocystis*, such as the number of segments in the terminal region of the hind tail, may be an artefact of preservation. The spines seem to represent an exception in this respect, as discussed below.

It can be shown that, at least in some cases, pyritization is partly responsible for the supposed observed differences in the morphology of spines, tail segments, and head plates, whereby aggregations of pyrite crystals or pyrite infillings causes variations in the width, section or outline of these structures. On the basis of the morphological data available, and of a comparison of the

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EXPLANATION OF PLATE 1

Figs 1–6. *Rhenocystis latipedunculata* Dehm, 1932; Bundenbach; Upper Pragian to Lower Emsian, *praecursor* dacryoconarid Zone; Hunsrückschiefer of Rhineland, Germany. 1, WB 514; juvenile specimen in dorsal aspect with complete tail. 2, BMNH EE 5886/5; complete dorsal head skeleton and partial tail. 3, DBM-HS 567; partially disrupted ventral head skeleton. 4, BMNH EE 5900; complete ventral head skeleton and partial tail. 5, BMNH EE 5901; complete ventral head skeleton and tail. 6, BMNH EE 5899 (cast of St 1928 VII 2, holotype); complete ventral head skeleton. All × 3.

PLATE 1


1


2


3


4


5


6

RUTA and BARTELS, *Rhenocystis*

new material of *Rhenocystis* with that figured by Dehm (1932, 1934), it is reasonable to assume that all the individuals of this mitrate belong to a single species.

A very small specimen in the collections of the Deutsches Bergbau-Museum, Bochum, provisionally labelled as WB 514 (Pl. 1, fig. 1), is likely to represent a juvenile of *Rhenocystis latipedunculata*, as revealed by its dorsal plating pattern (especially by the shape of the lateral margins of plates PM) and by the morphology of the hind tail. In comparison with adults of *Rhenocystis*, WB 514 possesses a less elongate head, larger lateral head walls, longer and more slender spines, and a longer and stouter hind tail. The hind tail has a smaller number of segments (about 26) in comparison with that of adult individuals (about 60); the ossicles of the first two segments, however, are much larger than those belonging to successive segments and comparable in size to the posterior styloid blade. The remaining hind tail segments change in size gradually along most of the length of the tail, whereas their shape is almost constant. In the distal quarter of the appendage, the ossicles are approximately as long as high and are hemicylindrical in shape. WB 514 is the only specimen whose hind tail is almost straight as preserved.

The head

The head of adult individuals of *Rhenocystis* is slightly longer than wide and box-shaped. It has a flat dorsal surface, a gently convex ventral surface, and two almost vertical, lateral walls which become progressively deeper antero-posteriorly (Text-figs 4–5). Several morphological details of the ventral head skeleton indicate that *Rhenocystis* has affinities with *Placocystites forbesianus* de Koninck, 1869 and *Victoriacystis wilkinsi* Gill and Caster, 1960 (see also Jefferies and Lewis 1978; Ruta 1997). *Mongolocarpos minzhini* Rozhnow, 1990 may also be closely related to *Placocystites*, *Rhenocystis* and *Victoriacystis* (see below).

In its general proportions, the head of *Rhenocystis* closely resembles that of *Victoriacystis*. Interestingly, in the smallest known specimen, WB 514 (Pl. 1, fig. 1), the head is about as long as wide. The same condition is also observed in juveniles and adults of *Placocystites*, as documented by Jefferies (1984).

Dorsal head skeleton (Text-figs 4B, 5A; Pl. 1, figs 1–2; Pl. 2, fig. 4; Pl. 3, fig. 3; Pl. 4, fig. 4; Pl. 5, figs 4–5; Pl. 6, fig. 1; Pl. 7, figs 1, 3; Pl. 8, fig. 1; Pl. 9, fig. 3). The dorsal head skeleton is composed of 11 marginal and two centro-dorsal plates. The marginal plates are divided into a group of six lateral elements arranged in pairs, an anterior transverse row composed of three elements framing the mouth opening dorsally, and a posterior group of two elements in contact with each other mid-dorsally.

The six lateral marginal plates comprise an anterior or distal pair (DLM) which gives insertion to the oral spines (see below); an intermediate pair (ILM) which occupies most of the length of the left and right lateral head margins; and a posterior or proximal pair (PLM) which contributes to the posterior head excavation (Text-figs 4B, 5A). Each of the lateral marginal plates is divided morphologically into a dorsal, horizontal part and a lateral, almost vertical part, meeting at an angle of about 90°. Restoration of deformed specimens and accurate delimitation of plate boundaries in several distorted individuals show that *Rhenocystis* does not possess sharp lateral head margins, as hypothesized by Dehm (1932) on the basis of a comparison with *Placocystites*. In dorso-ventrally compressed specimens, the lateral head walls lie flush with either the ventral or the dorsal head skeleton, and can be mistaken for folded parts of the ventral surface (e.g. Pl. 1, figs 1–6; Pl. 4, figs 4–6; Pl. 5, fig. 4; Pl. 7, figs 2–3; Pl. 8, fig. 4).

The anterior, transverse row of dorsal marginal plates (MOP and left and right LOP) is flexibly articulated with the centro-dorsal elements A and C, and with the left and right DLM (Pl. 1, fig. 2; Pl. 4, fig. 4; Pl. 7,

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EXPLANATION OF PLATE 2

Figs 1–4. *Rhenocystis latipedunculata* Dehm, 1932; Bundenbach; Upper Pragian to Lower Emsian, *praecursor* dacryoconarid Zone; Hunsrückschiefer of Rhineland, Germany. 1, DBM-HS 567; anterior half of ventral head skeleton and spines. 2, DBM-HS 566; spine morphology. 3, DBM-HS 564; complete, but heavily deformed ventral head skeleton, complete spines and ventral sculpture. 4, DBM-HS 750; anterior half of slightly disrupted dorsal head skeleton, with possible articulation tubercle for the left oral spine on the left DLM; note the finely tapering spines and the shape of the left ILM. All × 5.


1


2


3


4

RUTA and BARTELS, *Rhenocystis*

figs 1, 3). Such flexible articulation is also present in *Victoriacystis* (Gill and Caster 1960; Ruta 1997) and in the austral Allanicytidiidae (Caster 1954, 1983; Caster and Gill 1968; Philip 1981; Haude 1995; Ruta and Theron 1997). Preliminary results of a cladistic analysis by the senior author show that a flexible upper lip evolved in parallel in the clade (*Rhenocystis latipedunculata* + *Victoriacystis wilkinsi*) and in Allanicytidiidae (*contra* Ruta and Theron 1997). In *Victoriacystis*, MOP and LOP possess a slightly pronounced ridge along their posterior margins, which fits into a shallow groove on the anterior margins of A, C, and of the left and right DLM. Some specimens of *Rhenocystis* show a similar, although less evident articulation between plates MOP and LOP and the plates lying immediately posterior to them. The relative flexibility of the anterior dorsal region of the head may explain why the latter is often found disrupted to a larger extent than the rest of the skeleton. The left and right LOP are sub-triangular in outline, and show a gently curved anterior margin; MOP is sub-rectangular with an almost straight anterior margin. Unlike *Victoriacystis*, *Rhenocystis* does not have a knobbly ornament on MOP.

The left and right PM are much longer than wide. The proximal quarter of their lateral margins turns abruptly medianward. Their posterior margins are almost straight and are longer than their anterior margins. These are slightly convex towards C, and join the latter forming three angles of 120°. Plates PM contribute to the tail insertion together with the left and right PLM, V20 and V22 (Text-figs 4B, 5A; Pl. 1, fig. 2; Pl. 4, fig. 3; Pl. 7, fig. 3; Pl. 8, fig. 1), and resemble their homologues in *Victoriacystis* in their general proportions.

Plate A, or anomalocystid plate (Caster 1952), is wider anteriorly than posteriorly. As in most anomalocystidids (and in some mitrocystitids), A lies close to the left anterior angle of the dorsal skeleton, surrounded by the left LOP, DLM and ILM, and by C (Text-figs 4B, 5A; Pl. 1, fig. 2; Pl. 4, fig. 3; Pl. 7, figs 1, 3). The suture between A and C is gently convex postero-medially, more so than in *Victoriacystis*, but less so than in *Placocystites*. C reaches its maximum width at the level of its anterior third, where it contacts A and the right DLM.

The sculpture of the dorsal head skeleton consists of transversely elongate, widely spaced, robust ridges which, as usual in mitrates, show a steeper anterior slope and a gentler posterior slope (cuesta-shaped ribs of Jefferies 1986) (Text-fig. 4B; Pl. 1, fig. 2; Pl. 3, fig. 3; Pl. 5, figs 4–5; Pl. 6, fig. 1; Pl. 7, figs 1, 3; Pl. 8, fig. 1; Pl. 9, fig. 3). The ridges occupy the dorsal surface of the left and right PLM and those parts of the lateral head surfaces formed by the vertical extensions of plates PLM and, sometimes, ILM. Eight to 12 ridges are visible on both the left and the right PLM. The four or five most posterior ridges are more closely spaced than the remaining ridges and are orientated at an angle with respect to the longitudinal axis of the head. A few short ridges are visible near the posterior half of the lateral margins of plates PM in some specimens. The ridges on the vertical parts of plates PLM seem to correspond in number and position with those on their dorsal surfaces (see also Jefferies and Lewis 1978; Ruta 1997). The dorsal and lateral ridges occasionally show a sinuous course. When this condition occurs, they tend to break up irregularly (e.g. Pl. 6, fig. 1). Three or four ribs are sometimes visible on the posterior third of the vertical parts of plates ILM and, more rarely, on their dorsal parts.

Ventral head skeleton (Text-figs 4C, 5B; Pl. 1, figs 3–6; Pl. 2, figs 1, 3; Pl. 3, figs 1, 4–5; Pl. 4, figs 2–3, 5–6; Pl. 5, figs 1–3; Pl. 6, figs 3–4; Pl. 7, fig. 2; Pl. 8, figs 3–4; Pl. 9, figs 1, 4). The ventral head skeleton consists of 20 plates arranged in five transverse rows (Dehm 1932). These are numbered antero-posteriorly using Roman numerals (see also Ruta 1997; Ruta and Theron 1997).

Row I is five-plated (Pl. 1, figs 4–6; Pl. 4, figs 3, 6; Pl. 5, figs 1–2). For Dehm (1932, 1934), three plates (labelled as plates 5) were present in life, but his interpretation was certainly a result of different modes of preservation in different specimens, as well as disruption of row I. The two lateral plates, V1 and V5, are small, sub-trapezoidal elements, not always clearly visible in the available specimens. Sometimes, they are found superimposed on the admedian plates V2 and V4 (Pl. 2, fig. 3; Pl. 7, fig. 2; Pl. 9, fig. 1). Often, they are displaced

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EXPLANATION OF PLATE 3

Figs 1–5. *Rhenocystis latipedunculata* Dehm, 1932; Bundenbach; Upper Pragian to Lower Emsian, *praecursor* dacryoconarid Zone; Hunsrückschiefer of Rhineland, Germany. 1, DBM-HS 567; posterior half of disrupted ventral head skeleton. 2, BMNH EE 5886/3; spine morphology. 3, BMNH EE 5886/8; partially disrupted specimen in dorsal aspect with partial tail. 4, DBM-HS 524; partially preserved ventral head skeleton and complete hind tail. 5, DBM-HS 299; almost complete ventral head skeleton, complete spines, partially exposed fore tail and disrupted proximal region of the hind tail. Figs 1–2, ×5; figs 3–5, ×3.

PLATE 3


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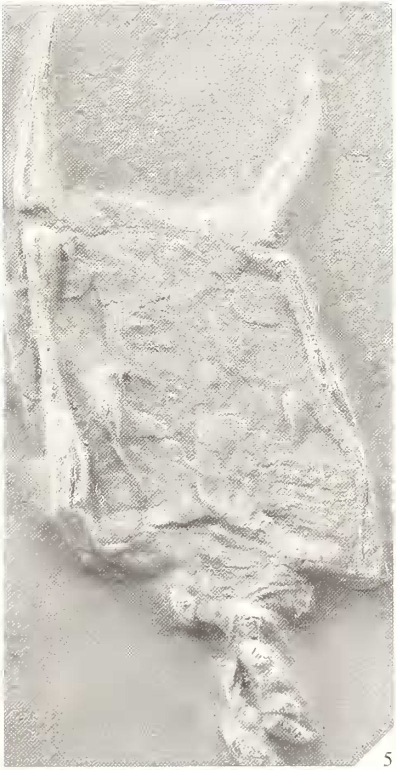
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RUTA and BARTELS, *Rhenocystis*

or partly covered by the surrounding elements (Pl. 1, fig. 3; Pl. 2, fig. 1; Pl. 4, fig. 5; Pl. 5, fig. 3; Pl. 9, fig. 4). The admedian plates, V2 and V4, are sub-pentagonal in outline and three to four times as large as V1 and V5. The mid-ventral plate, V3, is sub-trapezoidal. Its postero-lateral angles are truncated and form two short sutures with the admedian plates of row II. Its lateral margins are sometimes straight or, more often, gently concave outward, and converge slightly anteriorly. Its posterior margin is sutured with V12, and is one-third to one-half the maximum width of V3.

Row II consists of four plates, labelled as V6–V9 (plates 4 of Dehm 1932), approximately as large as or only slightly larger than V1 and V5, and sub-pentagonal in outline (Text-figs 4c, 5b; Pl. 1, figs 4–6; Pl. 4, figs 3, 6; Pl. 5, figs 1–2; Pl. 7, fig. 2; Pl. 9, fig. 1). V7 and V8 are much wider than long, whereas V6 and V9 are approximately as long as wide. Plates V6–V9 constitute the most distinctive feature of the ventral head skeleton of *Rhenocystis*, as they partially separate row I from row III. In such forms as *Bokkeveldia oosthuizeni* Ruta and Theron, 1997 and *Victoriacystis* (see Ruta 1997), row II is completely inserted between rows I and III. The new material of *Rhenocystis* confirms most of Dehm's (1932, 1934) observations on the shape and relative position of V6–V9. However, we could find no evidence of complete separation between V6 and V7 or between V8 and V9, except perhaps in the holotype, although the disrupted ventral skeleton of this specimen makes it difficult to delimit the plate boundaries accurately (Pl. 1, fig. 6). The V6/V7 and V8/V9 sutures are orientated obliquely with respect to the longitudinal axis of the head.

The three plates of row III, V10, V12 and V14 (plates 3 of Dehm 1932), are the largest elements of the anterior half of the ventral skeleton (Text-figs 4c, 5b; Pl. 1, figs 3–6; Pl. 2, figs 1, 3; Pl. 3, figs 1, 4–5; Pl. 4, figs 2–3, 5–6; Pl. 5, figs 1–2; Pl. 6, figs 3–4; Pl. 7, fig. 2; Pl. 9, figs 1, 4). V12 is octagonal and slightly longer than wide. Its posterior angle is truncated by V17 (see below). V12 and V14 are seven-sided plates with an irregular outline. The presence of a transverse row of three large polygonal elements just anterior to the centre of the ventral head skeleton also characterizes *Mongolocarpos*, *Placocystites* and *Victoriacystis* (Jefferies and Lewis 1978; Rozhnov 1990; Ruta 1997).

Row IV consists of five plates, V15–V19 (plates 2 of Dehm). As in *Placocystites forbesianus* and *Victoriacystis*, the sutures between V15 and V16 and between V18 and V19 are slightly convex medianward (Jefferies and Lewis 1978; Ruta 1997) (Text-figs 4c, 5b; Pl. 1, figs 5–6; Pl. 4, fig. 6; Pl. 5, fig. 2; Pl. 7, fig. 2). The central element, V17 or placocystid plate (Caster 1952), is unusually large in comparison with its homologue in such anomalocystitids as *Placocystites* and *Victoriacystis*, its size being comparable to or greater than that of V16 and V18 (Pl. 1, figs 4–6; Pl. 2, fig. 3; Pl. 3, fig. 4; Pl. 4, figs 2, 6; Pl. 5, fig. 2; Pl. 6, fig. 3; Pl. 8, fig. 3). In other anomalocystitids, V17 varies in shape, size and relative position with respect to the surrounding plates (Ubaghs 1979; Kolata and Jollie 1982; Jefferies 1984; Craske and Jefferies 1989; Parsley 1991; Ruta 1997). V12, V16, V18 and V21 are truncated where they abut against V17.

Row V consists of three plates, V20–V22. V20 and V22 (plates b of Dehm) are in contact with each other along a short suture lying immediately posterior to V21, and are the largest elements of the posterior half of the ventral skeleton (Text-figs 4c, 5b; Pl. 1, figs 3–6; Pl. 2, fig. 3; Pl. 3, figs 1, 4–5; Pl. 4, figs 2–3, 5–6; Pl. 5, figs 2–3; Pl. 6, fig. 3; Pl. 7, fig. 2; Pl. 8, figs 3–4). Posteriorly, they contribute to the head excavation for the tail insertion. Their lateral margins are gently sinuous, and turn abruptly away from the longitudinal axis of the head at the level of their posterior third, when observed in ventral view. V20 and V22 are similar in general proportions and relative size to the corresponding plates in *Victoriacystis*, but are more elongate than their homologues in *Placocystites*. V21 (plate v of Dehm) is a shield-shaped element, only slightly longer than wide and rhomboidal in outline. Its postero-lateral margins are not uniformly convex outward, but show a sudden change in curvature in the distal part of their posterior third. The antero-lateral margins are much shorter than the postero-lateral margins, and gently convex anteriorly, as in *Placocystites*.

EXPLANATION OF PLATE 4

Figs 1–6. *Rhenocystis latipedunculata* Dehm, 1932; Bundenbach; Upper Pragian to Lower Emsian, *praecursor* dacryoconarid Zone; Hunsrückschiefer of Rhineland, Germany. 1, BMNH E 23660; anterior, intermediate and part of the posterior regions of the hind tail in left lateral aspect. 2, DBM-HS 564; general aspect of the ventral head skeleton, distribution of the ventral sculpture and well-preserved hind tail. 3, DBM-HS 301; partially preserved plate arrangement in the anterior half of the ventral head skeleton, complete spines and extensive overlap of some fore tail rings. 4, BMNH EE 5886/2; partially preserved dorsal head skeleton and complete spines. 5, DBM-HS 297; complete, but heavily disrupted ventral skeleton and complete tail. 6, DBM-HS 300; complete ventral head skeleton and partially exposed hind tail. Fig. 1, ×5; figs 2–6, ×3.


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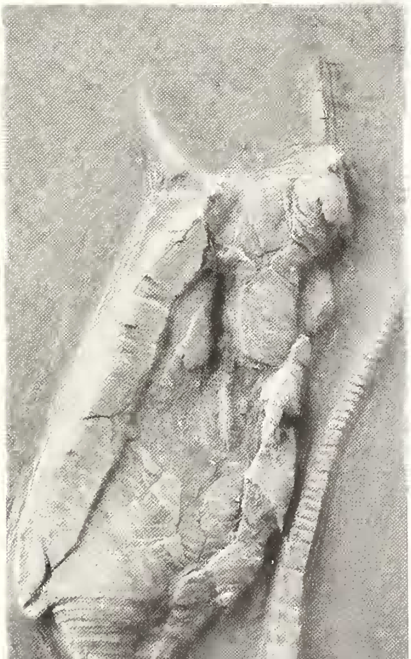
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RUTA and BARTELS, *Rhenocystis*

The sculpture of the ventral head skeleton is usually confined to row V, although some specimens show short ridges near the posterior-lateral angles of V15 and V19 and/or near the postero-median angles of V16 and V18 (Text-fig. 4A, C, E; Pl. 1, figs 3–6; Pl. 2, fig. 3; Pl. 3, figs 1, 4–5; Pl. 4, figs 2, 5–6; Pl. 5, figs 2–3; Pl. 6, fig. 3; Pl. 7, fig. 2; Pl. 8, figs 3–4; Pl. 9, fig. 4). As in the case of the dorsal head skeleton, the ridges are comparatively more robust than in other anomalocystitids, and less numerous. Although the morphology of the posterior half of its ventral head skeleton recalls that of *Victoriacystis* (see Gill and Caster 1960; Ruta 1977), *Rhenocystis* differs from the latter in that its ventral ridges (especially those on V20 and V22) are more irregular posteriorly, where they delimit two transversely elongate, smooth areas near to the posterior margins of V20 and V22. These areas, also visible in *Placocystites* and *Victoriacystis*, delimit a change in the curvature of V20 and V22 (Jefferies and Lewis 1978; Jefferies 1984; Parsley 1991; Ruta 1997).

The spines (Text-fig. 4A–C; Pl. 1, figs 1–6; Pl. 2 figs 1–4; Pl. 3, figs 2–5; Pl. 4, figs 2–6; Pl. 5, figs 1–5; Pl. 6, fig. 4; Pl. 7, figs 1–3; Pl. 8, fig. 4; Pl. 9, figs 1, 4). As noted by Dehm (1932, 1934), the spines of *Rhenocystis* (called horns by Dehm) vary considerably in shape and relative size. In most specimens, they are approximately as long as the anterior head margin, and show a slightly convex, sharp, lateral edge and a concave, blunt, median edge. This morphology is also found in *Placocystites* (Jefferies and Lewis 1978; Jefferies 1984). In cross section, the spines are roughly elliptical, the greater axis of the cross section being horizonal.

In some specimens, however, the spines are almost straight, cigar-like, and slightly shorter than the anterior head margin. In some cases, this shape results from the fact that the spines are not fully exposed. The finely drawn-out and slender spine shape observed by Dehm (1934) in a few specimens is almost certainly due to deformation without breakage. In addition, the extensive degree of pyritization often cancels any sign of breakage, resulting in uniformly tapering spine stumps.

The spines are slightly expanded proximally. A comparison with other anomalocystitids suggests that a socket was present on their proximal surface (Pl. 1, figs 2–3, 5; Pl. 2, fig. 1; Pl. 3, fig. 2; Pl. 7, fig. 3). The latter accommodated a toroidal process visible in some specimens on the anterior surface of the left and right DLM (Text-figs 4D, 5B; Pl. 1, figs 2, 5; Pl. 3, fig. 5; Pl. 4, fig. 4; Pl. 7, figs 1, 3). The presence of a space between the spine insertion and the lateral margin of each of the two plates LOP, as well as between the spine insertion and the antero-lateral angles of the left and right DLM, suggests that, as in *Placocystites*, a fold of integument was probably wrapped around the base of each spine (see Jefferies and Lewis 1978 for a functional interpretation of this integument). However, no direct evidence of such a fold can be observed in *Rhenocystis*.

The spines may have acted as a supporting and steering device in life. Their sharp, lateral edge probably cut a way open through the sediment during the lateral stroke. A similar function was hypothesized by Jefferies and Lewis (1978) and Jefferies (1984) for *Placocystites*, whose spine morphology recalls that of *Rhenocystis*.

The tail

As in all mitrates, the tail of adult individuals of *Rhenocystis* is divided into fore (proximal), mid (intermediate) and hind (distal) tail in order of increasing distance from the posterior head excavation. Articulated specimens in different orientations with respect to the bedding planes allow an accurate reconstruction of the external aspect of the tail. Its internal features, however, are not known, as isolated tail segments have not been found and the lumen of broken tails is usually filled with pyrite crystals or framboids which obliterate its fine morphological details.

In the smallest known specimen, WB 514 (Pl. 1, fig. 1), the anteriormost hind tail segments show well-differentiated dorsa ossicular processes which are larger than those belonging to more posterior segments (see

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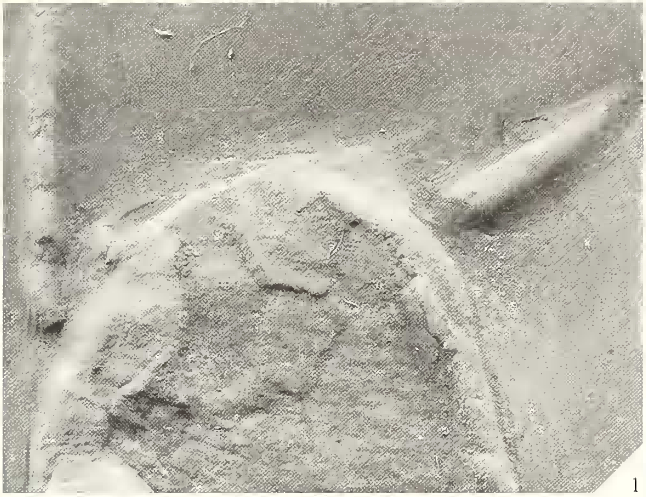
EXPLANATION OF PLATE 5

Figs 1–5. *Rhenocystis latipedunculata* Dehm, 1932; Bundenbach; Upper Pragian to Lower Emsian, *praecursor* dacryoconarid Zone; Hunsrückschiefer of Rhineland, Germany. 1, DBM-HS 301; slightly deformed anterior third of the ventral head skeleton with complete spines. 2, BMNH E 29316; complete, articulated ventral head skeleton and partially exposed fore and hind tail. 3, DBM-HS 296; disrupted ventral head skeleton and tail. 4, DBM-HS 750; showing a fully exposed and exceptionally well preserved tail; the right half of the dorsal head skeleton is folded and crushed. 5, BMNH EE 5898; showing almost complete, but partly disrupted dorsal head skeleton, a broken left spine and a complete tail. Fig. 1, ×6; figs 2–5, ×3.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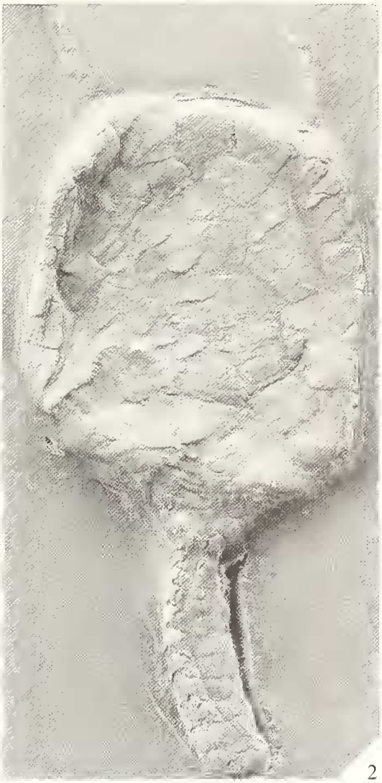
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above). Conversely, the posteriormost segments are much simpler in shape. These features suggest that during growth, new segments were probably added at the distal tip of the hind tail.

The fore tail: morphology (Text-figs 4A–C, 6; Pl. 1, figs 1–2, 4–6; Pl. 2, fig. 3; Pl. 3, figs 3, 5; Pl. 4, figs 2–3, 5; Pl. 5, figs 2, 4–5; Pl. 6, fig. 1; Pl. 7, fig. 3; Pl. 8, figs 1, 3). The fore tail skeleton is composed of tetramerous rings. A maximum of eight rings can be observed in the best preserved specimens, although, as in the case of several other anomalocystitids, their precise number is uncertain. The width of the rings, but not their height, decreases rapidly antero-posteriorly; as a result, the fore tail is about three times as wide near the junction with the head as near the insertion of the mid tail (Text-fig. 4B–C, E; Pl. 1, figs 2, 4–5; Pl. 2, fig. 3; Pl. 3, fig. 3; Pl. 4, figs 2, 5; Pl. 5, figs 2, 4–5; Pl. 7, fig. 3; Pl. 8, figs 1, 3). The cross section of the fore tail is difficult to reconstruct due to compaction and distortion.

A comparison with *Victoriacystis* (Gill and Caster 1960; Ruta 1997) suggests that in *Rhenocystis*, the most anterior rings are sub-elliptical and strongly compressed dorso-ventrally, whereas the most posterior rings are sub-circular. Each ring overlaps its posterior neighbour. The degree of overlap is greater in the anterior half of the fore tail than in the posterior half.

In some specimens, a fold of polyplated, presumably flexible integument is partly visible between each ring (Pl. 2, fig. 3; Pl. 4, figs 2, 5; Pl. 5, fig. 4; Pl. 6, figs 1–2; Pl. 8, figs 1, 3). The plates of the integument are small and transversely elongate. The distal margin of each fold occupies a narrow gap present between each of the four ring plates and the corresponding plates of the next posterior ring (Text-figs 4A, 6A). This gap results from a proximo-distal shortening of the median half of each plate. An irregular thickening runs along the distal margins of the ring plates.

Anteriorly in the fore tail, the two dorsal plates of each ring are smaller than the two ventral plates, but such difference in size is not significant in the two most posterior rings. The degree of curvature of the ventral plates is greater than that of the dorsal plates throughout the fore tail length; as a result, the external surface of the ventral plates contributes to about two-thirds of the lateral aspect of the fore tail. In each ring, the two dorsal plates are in contact with each other mid-dorsally along a vertical and presumably flat surface; likewise, the two ventral plates are rigidly sutured mid-ventrally. Each dorsal plate forms a rocking articulation with the ventral plate of the same side. In those specimens in which the fore tail is dorso-ventrally compressed, flexed laterally or disrupted as a result of compaction, the dorsal and ventral fore tail plates are sometimes found separated, allowing some morphological details of their articulation surfaces to be observed (Pl. 1, fig. 2; Pl. 3, fig. 3; Pl. 5, figs 4–5; Pl. 7, fig. 3; Pl. 8, fig. 1).

The dorso-lateral end of each ventral plate is slightly expanded antero-posteriorly and thickened with respect to the rest of the plate. Its articulation surface slopes downward in a latero-median and in an antero-posterior direction. The articulation surface is elliptical to rounded in outline in dorsal aspect, and carries a transversely elongate, shallow pit which occupies its posterior half (Text-fig. 6B). None of the specimens examined shows the articulation surface of the dorsal plates. However, in those specimens in which the fore tail is strongly flexed lateralward, a small, rounded knob is visible near the posterior half of the ventro-lateral end of each dorsal plate; this knob fits into the shallow pit of the articulation surface of the ventral plate of the corresponding side (Pl. 1, fig. 2; Pl. 3, fig. 3; Pl. 7, fig. 3; Pl. 8, fig. 1).

The fore tail: function. Rhenocystis could presumably flex its fore tail to a considerable extent, both in the horizontal and in the vertical plane, as indicated by several details of the constructional morphology of the fore tail rings and by the modes of preservation of many specimens. The degree of overlap, as well as the large size of the proximal fore tail rings and the presence of rocking articulations between dorsal and ventral fore tail plates, are also observed in *Victoriacystis* (Gill and

EXPLANATION OF PLATE 6

Figs 1–4. *Rhenocystis latipedunculata* Dehm, 1932; Bundenbach; Upper Pragian to Lower Emsian, *praecursor* dacryoconarid Zone; Hunsrückschiefer of Rhineland, Germany. 1, DBM-HS 570; showing complete hind tail with coiled distal end; ×4. 2, DBM-HS 750; close-up of the mid and hind tail, mainly in right lateral aspect; ×5. 3, DBM-HS 524; close-up of hind tail and posterior sculpture of the ventral head skeleton; ×5. 4, BMNH EE 5902; partially preserved ventral skeleton and complete hind tail; ×3.


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RUTA and BARTELS, *Rhenocystis*

Caster 1960; Ruta 1997). Folds of flexible, polyplated integument between each fore tail ring were described by Jefferies and Lewis (1978) in *Placocystites*, and by Kolata and Guensburg (1979) in *Diamphidiocystis drepanon*. They are probably present also in *Enoploura popei* Caster, 1952 (Parsley 1991) and *Placocystella africana* (Reed, 1925) (Ruta and Theron 1997). Fore tail integument folds were not observed by Ruta (1997) in *Victoriacystis*, although this may be due to preservation.

The folds of polyplated integument are comparatively less expanded antero-posteriorly in *Rhenocystis* than in *Placocystites*, and there is no evidence that they were strongly recumbent posteriorly in the former. The dorsal and ventral integument folds of *Rhenocystis* do not differ appreciably in size; this indicates that the fore tail was perhaps equally flexible both dorsalward and ventralward. Conversely, the integument folds of *Placocystites* are particularly well developed on the dorsal surface of the fore tail, and may have enabled the latter to flex mainly towards the ventral head surface (Jefferies and Lewis 1978; Savazzi *et al.* 1982; Jefferies 1984; Savazzi 1994).

As in *Victoriacystis*, the lateral rocking articulations probably allowed the dorsal and ventral fore tail plates of *Rhenocystis* to rotate about a transverse axis relative to each other (Ruta 1997). Lateral movements of the dorsal and ventral plates were probably hindered by the oblique orientation of their articulation surfaces. Such orientation may also have prevented dorso-ventral deformation of the fore tail rings. Additional strength may have been provided by the mid-dorsal and mid-ventral sutures. The fore tail rings were likely to act both as rigid and as flexible units, enabling the tail to perform a wide variety of movements.

The mid tail: morphology (Text-fig. 4A–B; Pl. 1, figs 1–2; Pl. 3, fig. 3; Pl. 5, fig. 4; Pl. 6, figs 1–2, 4; Pl. 7, fig. 3; Pl. 8, fig. 1; Pl. 9, fig. 2). The skeleton of the mid tail consists of a massive element, the styloid, and its associated paired plates. As in other mitrates, the number of plates is difficult to determine (Kolata and Jollie 1982; Parsley 1991; Beisswenger 1994; Ruta 1997; Ruta and Theron 1997). The styloid is generally poorly preserved. A small process, partly visible in some disrupted specimens (e.g. Pl. 1, fig. 2; Pl. 7, fig. 3), projects from the styloid antero-ventrally. The process probably occupied the posterior part of the fore tail lumen, where it probably gave insertion to muscles in life. The dorsal and lateral surfaces of the styloid are observed only in few individuals.

The styloid is slightly longer than wide and bears two dorsal blades which differ in shape and size, and are separated by the broad, saddle-like dorsal styloid surface (Text-fig. 4A–B; Pl. 1, figs 1–2; Pl. 3, fig. 3; Pl. 5, fig. 4; Pl. 6, fig. 2). The maximum width of the styloid is at the level of its anterior blade. The anterior blade is broadly semicircular in outline in dorsal aspect, anteriorly recumbent in position, and carries a sharp, mid-dorsal keel. The keel fades gradually in a proximal direction and disappears before reaching the free margin of the anterior blade. Distally, it merges into the posterior blade. The posterior blade is much higher and stouter than the anterior blade, and broadly rectangular in lateral aspect. Its anterior margin is sigmoidal in lateral view, and does not seem to have been sharp. In none of the specimens examined is the posterior blade completely visible. Dorsally, the posterior blade shows a blunt apex. From the dorsal apex, the posterior surface of the blade widens progressively ventralward, but its articulation surface is not visible. The lateral surfaces of the blade are slightly depressed in their dorsal third, and become gently convex outward before merging into the lateral walls of the styloid.

The mid tail: function. The styloid of *Rhenocystis* closely resembles that of *Victoriacystis* in its general proportions and in the shape and relative size of its two blades (Gill and Caster 1960; Ruta

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EXPLANATION OF PLATE 7

Figs 1–5. *Rhenocystis latipedunculata* Dehm, 1932; Bundenbach; Upper Pragian to Lower Emsian, *praecursor* dacryoconarid Zone; Hunsrückschiefer of Rhineland, Germany. 1, DBM-HS 570; complete, but highly deformed dorsal head skeleton; ×4. 2, BMNH E 23660; general aspect of the ventral head skeleton; ×3. 3, BMNH EE 5886/1; complete but heavily damaged dorsal head skeleton and partial tail; ×3. 4, BMNH EE 5886/3; showing variation in the morphology of the hind tail segments; ×3. 5, DBM-HS 524; close-up of the distal part of the intermediate region of the hind tail; ×20.


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RUTA and BARTELS, *Rhenocystis*

1997). The styloid may have enhanced leverage of the tail in life, separating two regions, the fore and the hind tail, with different mechanical properties (Parsley 1991; Ruta 1997). The recumbent anterior blade and the dorsal keel were probably scarcely effective in life as anchoring devices. However, the massive posterior blade and the proximal hind tail ossicles were probably suitable for this function (see also discussion below).

The hind tail: morphology (Text-fig. 4A–C; Pl. 1, figs 1–2, 4–5; Pl. 3, figs 3–5; Pl. 4, figs 1–3, 5–6; Pl. 5, figs 2–5; Pl. 6, figs 1–4; Pl. 7, figs 3–5; Pl. 8, figs 1–4; Pl. 9, figs 2–4; Pl. 10, figs 1–5). The hind tail skeleton is composed of segments, each consisting of a dorsal ossicle and a pair of ventral plates articulated with it, and shows significant morphological variation throughout its length. Proximo-distally, the hind tail can be divided into an anterior, an intermediate, a posterior and a terminal region.

The anterior region of the hind tail consists of five or six segments characterized by the remarkable development of the dorsal ossicles (Text-fig. 4A; Pl. 5, fig. 4; Pl. 6, figs 2, 4; Pl. 8, fig. 1; Pl. 9, fig. 2). The ossicles decrease in size from the first to the fifth or sixth segment, but this decrease is not gradual. The height of the first three ossicles diminishes only to a small extent in passing from the first to the second and from the second to the third segment. The height of the fourth ossicle is about two-thirds that of the third ossicle. The fifth ossicle is only slightly smaller than the fourth. Finally, the sixth ossicle is about one-third the height of the first and is comparable in size and shape to the anterior ossicles of the intermediate region.

The ossicles of the anterior region are approximately equal in length. The first ossicle closely resembles the posterior styloid blade. Each of the first five or six ossicles can be divided morphologically into a ventral part, bearing an anterior and a posterior articulation surface, and a dorsal process. As isolated ossicles have not been found, the articulation surfaces cannot be reconstructed. The ventral parts of the four most anterior ossicles are connected to each other through a peg-and-socket mechanism, clearly visible in lateral view: in each ossicle, the lower half of the anterior margin of the ventral part shows a protruding knob, which fits into a shallow excavation of the posterior margin of the next anterior ossicle.

A similar articulation mechanism was described by Ruta (1997) in *Victoriacystis wilkinsi*, and by Ruta and Theron (1997) in *Placocystella africana*. In the ossicles of the intermediate region of the hind tail, the peg-and-socket articulation is less pronounced. In the posterior and terminal regions, the anterior and posterior ossicular margins are slightly sinuous to straight.

In cross section, the ossicles of the anterior region are gently convex externally in their lower third. The lateral surfaces of their ventral parts merge gradually into those of their dorsal processes; at this level, the lateral ossicular surfaces are slightly concave outward, but become almost vertical in the upper third of the processes. The dorsal margins of the processes do not seem to have been sharp. Their lateral surfaces merge anteriorly into a blunt, vertical margin. The dorsalmost part of their posterior surfaces is flat and roughly triangular. The ventral ossicular margins are vaguely chevron-shaped in lateral view. In the first three or four ossicles, the anterior arm of the chevron is much shorter than the posterior arm. In successive ossicles of the anterior region, as well as in the ossicles of the intermediate and of most of the posterior region of the hind tail, the ventral ossicular margins are likewise chevron-shaped, but the two arms of the chevron are subequal in length. The ventral ossicular margins of the distalmost ossicles are slightly convex ventralward to straight in lateral aspect.

The intermediate region of the hind tail consists of six or seven segments of approximately equal length. These differ from the segments of the anterior region in that the dorsal ossicular processes are comparatively much smaller and confined to the posterior third of the dorsal ossicular surface. From the apex of each process, the dorsal ossicular margin slopes anteriorly and slightly ventralward following a gently sinuous course. In the two or three posteriormost segments of the intermediate region, the dorsal ossicular processes are slightly inclined backward, so that the apex of each process slightly overhangs the posterior articulation surface of the

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EXPLANATION OF PLATE 8

Figs 1–4. *Rhenocystis latipedunculata* Dehm, 1932; Bundenbach; Upper Pragian to Lower Emsian, *praecursor* dacryoconarid Zone; Hunsrückschiefer of Rhineland, Germany. 1, DBM-HS 744; close-up of hind tail in left lateral aspect; × 5. 2, DBM-HS 566; anterior region of the hind tail in left lateral aspect; × 6. 3, DBM-HS 564; morphology of the tail and posterior sculpture of the ventral head skeleton; × 5. 4, BMNH EE 5890; incomplete ventral head skeleton and well-preserved hind tail; × 3.


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RUTA and BARTELS, *Rhenocystis*

corresponding ossicle (Text-fig. 4A; Pl. 1, fig. 5; Pl. 3, figs 2, 5; Pl. 5, figs 4–5; Pl. 6, figs 1–4; Pl. 7, fig. 4; Pl. 8, figs 1–4; Pl. 9, figs 2–4).

The posterior region of the hind tail is composed of five or six segments. The ossicles are approximately hemicylindrical and decrease uniformly in size in an antero-posterior direction. Their length is slightly greater than their width and the length/width ratio remains approximately constant. The ossicles bear a slightly pronounced, knob-like, postero-dorsal apex (Text-fig. 4A; Pl. 1, fig. 5; Pl. 3, fig. 4; Pl. 4, figs 1–2, 5; Pl. 5, figs 4–5; Pl. 6, figs 1–4; Pl. 7, fig. 4; Pl. 8, figs 1, 3–4; Pl. 9, figs 3–4).

In those adult specimens in which complete tails are preserved, the terminal region of the hind tail has a minimum of about 30 and a maximum of about 45 recorded segments. The ossicles of this region are approximately as long as wide and become progressively smaller antero-posteriorly. The postero-dorsal apex is either strongly reduced or absent. In lateral view, the anterior and posterior ossicular margins are almost straight, especially at the level of the last ten or 15 segments.

The modes of preservation of various specimens suggest that the terminal part of the hind tail was probably more flexible than the rest of the appendage. In some specimens, the terminal region is straight; in others, it is slightly bent dorsally; more commonly, it curves ventrally along a tight curve; in two individuals, its distalmost end is coiled (Text-fig 4A; Pl. 1, fig. 5; Pl. 3, fig. 4; Pl. 4, figs 2, 5; Pl. 5, figs 4–5; Pl. 6, figs 1–4; Pl. 7, figs 4–5; Pl. 8, figs 1, 3–4; Pl. 9, figs 2–4; Pl. 10, figs 1–5).

The paired ventral hind tail plates change gradually in shape and size from the anterior to the terminal region of the hind tail, and overlap each other antero-posteriorly. The degree of overlap increases from the anterior to the terminal region of the hind tail. In some specimens in which the hind tail is partly disrupted, the dorsal ossicles are visible in ventro-lateral aspect (Pl. 3, fig. 4; Pl. 4, fig. 2; Pl. 6, fig. 3; Pl. 8, fig. 3). A longitudinal, shallow groove runs on the ventro-lateral projections of the dorsal ossicles. This groove accommodates the dorsal margins of the ventral plates. When ossicles and plates are articulated with each other and are observed in lateral aspect, the grooves are not visible, since the lowermost part of the external surfaces of the ventro-lateral projections of each ossicle abuts against the upper part of the inside of the plates.

The ventral plates of the anterior, intermediate and part of the posterior regions of the hind tail are slightly longer than wide, and strongly arcuate in cross section (Text-fig. 4A, C). Their posterior margins are sinuous and slope ventralward and posteriorly in lateral aspect. The left and right plates meet along the mid-ventral line forming a gently rounded ventral surface. The plates of the distal part of the posterior region and those of the terminal region of the hind tail are roughly semicircular, almost as long as wide, and only slightly arcuate in cross section. Their posterior margins are convex.

In these two regions, the left and right plates meet at an obtuse angle mid-ventrally. Some specimens show that the distal ventral plates were arranged along two alternating rows, the right plates being slightly displaced anteriorly with respect to the corresponding elements of the left side (e.g. Pl. 6, fig. 2; Pl. 10, fig. 3). A knob is present near the dorsal margin of all ventral plates except those of the most anterior region of the hind tail. In the intermediate region, the knob is approximately equidistant from the anterior and the posterior margin of each plate (Pl. 6, fig. 2; Pl. 8, fig. 3; Pl. 10, figs 3–5). In the posterior and terminal regions, the knob is displaced slightly posteriorly. The plates of the anterior region show a dorsal, horizontal thickening (Pl. 8, fig. 1).

The hind tail: function. The large degree of overlap of the paired ventral plates in an antero-posterior direction and the preservation of several specimens suggest that the hind tail could be bent towards the ventral side of the head along a tight curve. Dorsal flexion was likely to occur in life, but probably to a lesser extent. The ossicles abut against each other when the tail is reconstructed in various degrees of dorsal flexion. The mechanical constraints imposed by the ossicles are especially evident in those mitrates in which the anterior and posterior ossicular surfaces as well as the

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EXPLANATION OF PLATE 9

Figs 1–4. *Rhenocystis latipedunculata* Dehm, 1932; Bundenbach; Upper Pragian to Lower Emsian, *praecursor* dacryoconarid Zone; Hunsrückschiefer of Rhineland, Germany. 1, BMNH E 23660; close-up of the anterior half of the ventral head skeleton and of the spines; ×6. 2, DBM-HS 298; hind tail morphology; ×4. 3, BMNH EE 5887; hind tail with characteristically bent distal quarter; ×5. 4, BMNH EE 5895; ventral head skeleton and articulated tail; ×3.


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RUTA and BARTELS, *Rhenocystis*

articulations between dorsal ossicles and ventral plates are known in detail (e.g. Jefferies 1967, 1968, 1973, 1986; Jefferies and Lewis 1978; Kolata and Jollie 1982; Ruta and Theron 1997), but are inferred to have existed also in *Rhenocystis*.

Mechanical constraints preventing the hind tail of *Rhenocystis* from achieving a high degree of dorsal flexion are more evident at the level of its anterior region, where the ossicles show remarkably well developed dorsal processes, and leave a narrow space between adjacent segments even when the hind tail is straight. More posteriorly, the degree of dorsal flexion was perhaps higher, as the processes are either poorly developed or absent.

In most mitrates the tail is often found flexed towards the ventral side of the head (Hall 1858; Caster 1954; Caster and Gill 1968; Kolata *et al.* 1991; Parsley 1991; Ruta 1997; Ruta and Theron 1997), but rare occurrences of dorsally bent hind tails are known (e.g. Kolata and Jollie 1982; Parsley 1991). If, as suggested by Jefferies (1986), most of the lumen of the hind tail housed muscles in life, these were presumably located mainly between the ventral plates and the ventro-lateral extensions of the dorsal ossicles. Post-mortem contraction of these muscles is expected to cause ventralward bending of the hind tail.

Although there is no direct evidence of the modalities of insertion of such muscles, it is reasonable to assume that each was connected to different segments in order to ensure mobility (Jefferies 1967, 1986; Kolata and Jollie 1982). Dorsal muscles and or ligaments are likely to have been present between the articulation surfaces of adjacent ossicles to counteract the action of the ventral muscles. Reconstructed cross sections of the hind tail segments in several mitrates (e.g. Jefferies 1967, 1968, 1986; Kolata and Jollie 1982; Ruta and Theron 1997) show that the estimated volume of the ventral muscles largely exceeded that of the dorsal muscles.

Elsewhere (Ruta 1997), it has been pointed out that the hypothesized functions of the various regions of the mitrate appendage differ to a considerable extent depending upon the affinities and life-style proposed for these animals (Ubaghs 1968; Philip 1981; Kolata and Jollie 1982; Jefferies 1984, 1986; Parsley 1991), but most arguments put forward to explain their life mode await corroboration. The morphology of the hind tail of *Rhenocystis* deserves further comments.

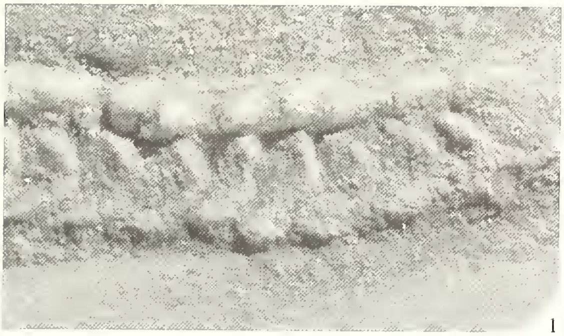
Almost certainly, the hind tail played an important rôle in the locomotion of the animal (Jefferies 1984). Its terminal and part of its posterior regions were certainly extremely flexible. The width of the tail was small compared with that of the head and, therefore, unlikely to have supplied a powerful thrusting action enabling the animal to drag itself along. The total surface area of the ventral plates seems to have been too small to provide an effective bearing surface, as in the model proposed by Jefferies (1984). If movement occurred at all, it was probably very disadvantageous energetically.

It is here proposed that, although rearward locomotion was plausible, as suggested by the kind and distribution of the head sculpture (Jefferies 1984, 1986), lateral rather than dorso-ventral thrusting actions of the tail were probably involved in the locomotory cycle. The lateral surfaces of the plates and ossicles of the anterior and intermediate regions of the hind tail may have provided the required bearing surface whereas the posterior and terminal regions were likely to act as a probing tool.

EXPLANATION OF PLATE 10

Figs 1–5. *Rhenocystis latipedunculata* Dehm, 1932; Bundenbach; Upper Pragian to Lower Emsian, *praecursor* dacryoconarid Zone; Hunsrückschiefer of Rhineland, Germany. 1, DBM-HS 750; distal end of the hind tail, showing overlapping plates. 2, DBM-HS 566; distal end of the hind tail, with overlapping plates and terminal segment. 3, DBM-HS 570; terminal hind tail region; note the shape and extensive overlap of the plates, the presence of a knob in a subcentral position near their dorsal margins, and the distal, coiled end. 4, DBM-HS 524; terminal hind tail region; note the arrangement of plates and ossicles and the distal end bending slightly ventralward and showing the terminal segment. 5, DBM-HS 564; terminal hind tail region and morphology of the distalmost ossicles. All × 20.

PLATE 10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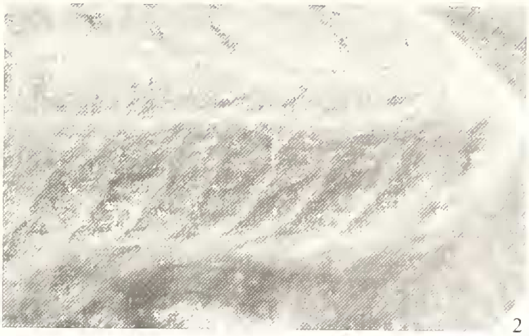
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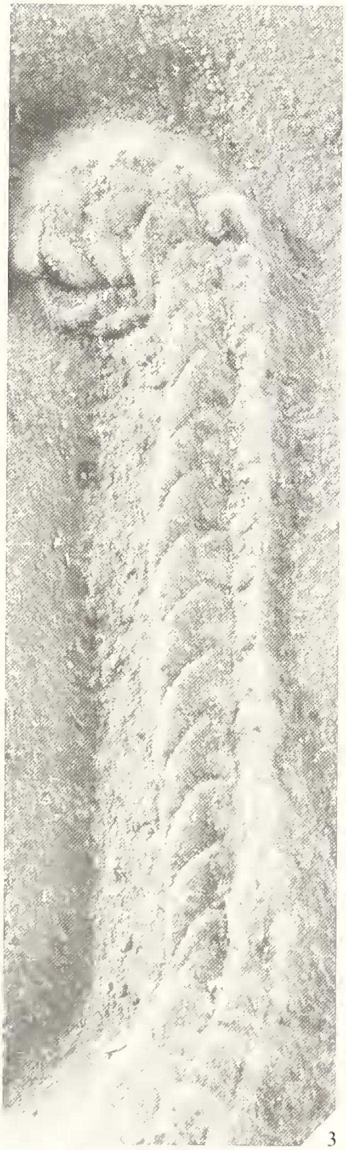
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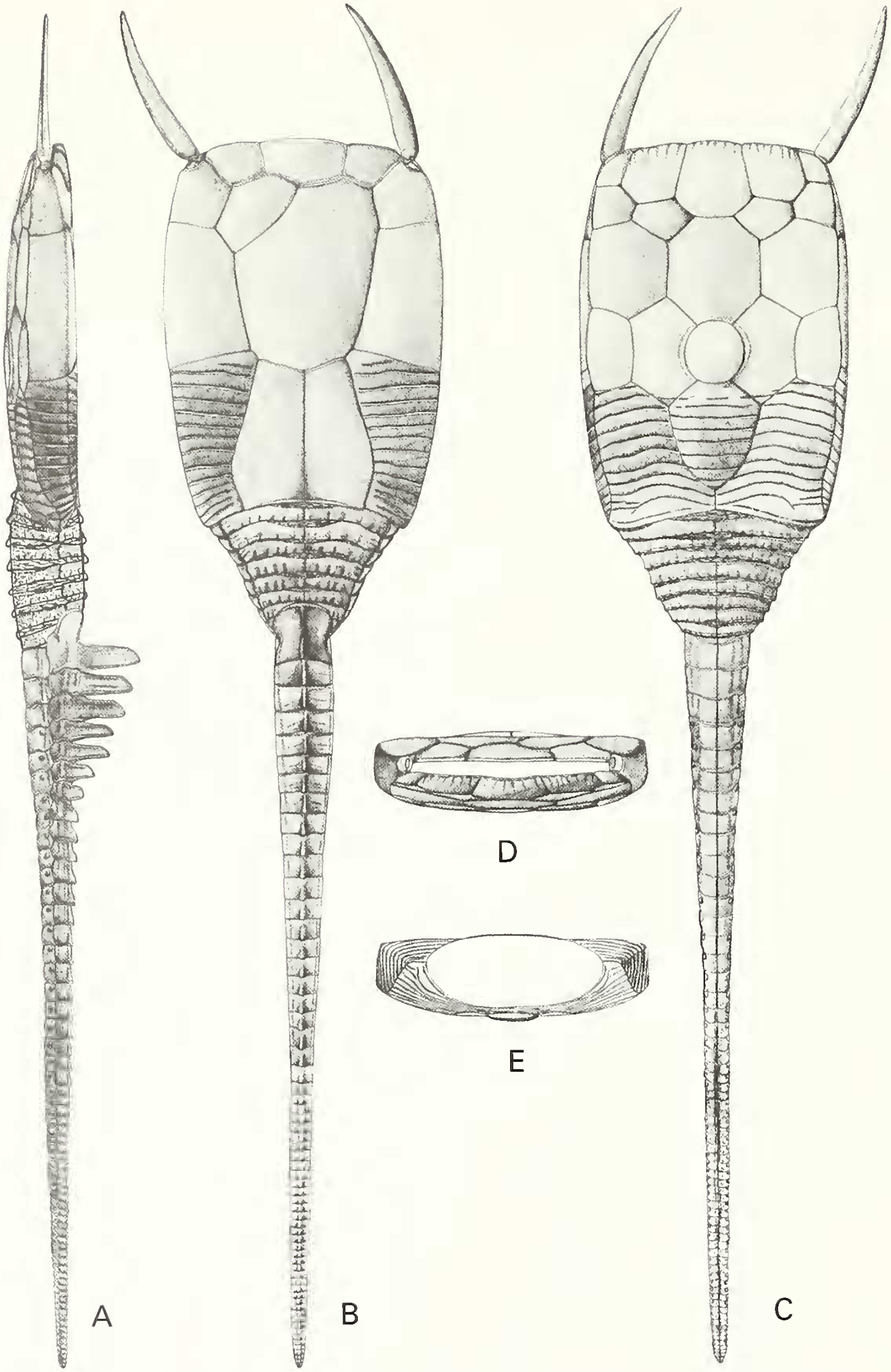
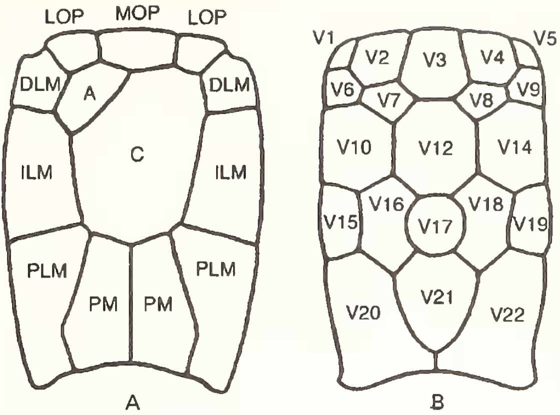
RUTA and BARTELS, *Rhenocystis*

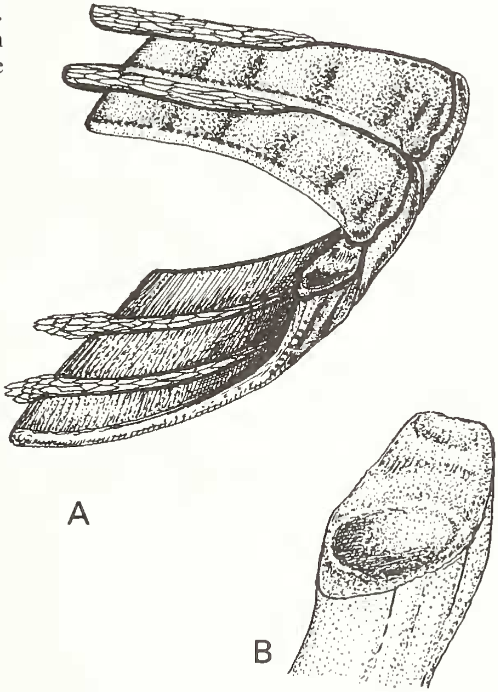


TEXT-FIG. 4. *Rhenocystis latipedunculata* Dehm, 1932. Reconstruction of the external skeletal morphology. A, left lateral view; B, dorsal view; C, ventral view; D, anterior view; E, posterior view.

TEXT-FIG. 5. *Rhenocystis latipedunculata* Dehm, 1932. Plate nomenclature. A, dorsal head skeleton; B, ventral head skeleton.



TEXT-FIG. 6. *Rhenocystis latipedunculata* Dehm, 1932. A, reconstruction of the rocking articulation between dorsal and ventral fore tail plates; B, sketch of the articulation surface of a ventral fore tail plate.



As regards life-style orientation, the ossicles of the anterior and part of the intermediate regions of the hind tail probably exerted the strongest bearing action when thrust down into the sediment and pushed against it laterally. *Rhenocystis* may have lived convex-side upward, probably just below the surface of the sea floor. The fore tail may have acted as the main motor during the locomotion, pushing alternatively leftward and rightward. Between each lateral thrust, the tail would be lifted up, partially freed from sediment, rotated in a direction opposite to that of the preceding lateral thrust and lowered down before performing the following lateral thrust.

The presence of well-developed lateral walls and the fact that the head was longer than wide suggest that yawing movements were probably limited during locomotion (see also Jefferies 1984). The general shape of the head and the distribution of the sculpture in mitrates were probably related to each other. In all of the anomalocystitids in which the length of the head is greater than its width, the sculpture (terrace-like ridges, pustules, riblets, etc.) occupies the proximal half or third of both the dorsal and the ventral surface of the head skeleton, or is strongly reduced (or even absent) on one or both of the two surfaces (e.g. *Enoploura*, *Rhenocystis* and *Victoriacystis*). Conversely, in those anomalocystitids in which the head is approximately as long as wide, the distribution of the sculpture is often more extensive (e.g. *Allanicytidium*, *Notocarpos* and *Placocystites*).

As suggested by Jefferies (1984), the gripping action of the most posterior ridges of both the dorsal and the ventral surface of *Rhenocystis* was perhaps mostly important in the initial phases of the locomotory cycle, and may have counteracted pitching movements of the head resulting from the downward thrust of the tail into the sediment.

AFFINITIES

Most of the works discussing mitrate classification and relationships predate the 'cladistic revolution' (Caster 1952; Gill and Caster 1960; Ubaghs 1968); they attempted to detect evolutionary trends in the absence of a comprehensive pattern of character distribution (Derstler 1979; Jefferies 1986, 1991; Craske and Jefferies 1989; Parsley 1991) or focused on only a small number of taxa (Philip 1981; Caster 1983; Ruta and Theron 1997).

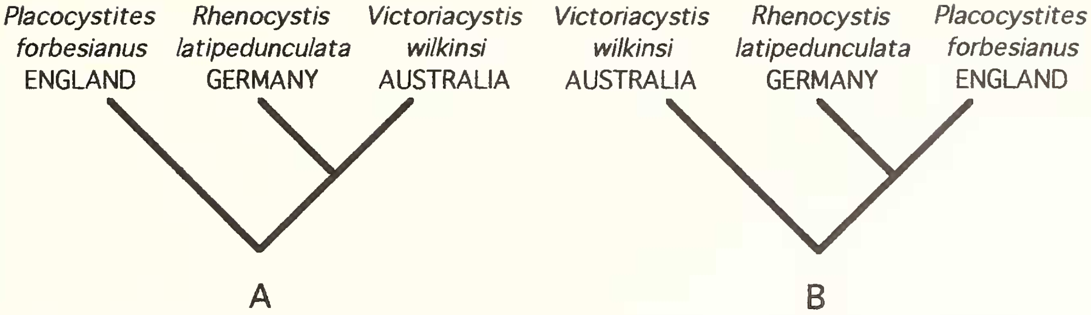
Since the publication of the carpoid volume of the *Treatise on invertebrate paleontology* (Ubaghs 1968), several new mitrate species have been described. Most of these belong to the Anomalocystitida as defined by Caster (1952) (Ubaghs 1968; Kolata and Guensburg 1979; Philip 1981; Kolata and Jollie 1982; Caster 1983; Regnault and Chauvel 1987; Rozhnov 1990; Parsley 1991; Haude 1995; Ruta and Theron 1997). Despite a few recent attempts to investigate the evolutionary history of this group (Parsley 1991; Ruta and Theron 1997), we are still far from reaching a consensus on its phylogeny. The monophyletic status of Anomalocystitida is likewise debated (e.g. Ubaghs 1979; Craske and Jefferies 1989; Parsley 1991; Beisswenger 1994; Ruta and Theron 1997).

Dehm (1932) assigned *Rhenocystis latipedunculata* to the family Anomalocystitidae (*nomen correctum* Bassler, 1938, *pro* Anomalocystidae Meek, 1872), together with the genera *Anomalocystites* Hall, 1858, *Enoploura* Wetherby, 1879, *Iowacystis* Thomas and Ladd, 1926 (transferred to the solutes by Bather in 1928; see Caster 1968) and *Placocystites* de Koninck, 1869. According to Dehm (1932), *Rhenocystis* and *Placocystites* constitute a well-characterized group within the Anomalocystitidae, due to their similar ventral plating patterns.

Caster (1952) placed *Placocystites* and *Rhenocystis* in the subfamily Placocystinae, which, together with Basslerocystinae and Enoplourinae, formed part of the family Placocystidae. Placocystidae was included by Caster (1952) in the suborder Placocystida, which comprised the vast majority of the anomalocystitid genera known at that time. The suborder Anomalocystida was erected by Caster (1952) to include the family Anomalocystitidae containing the single genus *Anomalocystites*. According to Caster (1952), *Rhenocystis* and *Placocystites* share the presence of two plastron somatic plates, A and Cs (plates A and C herein) and a placocystid plate (plate V17 herein).

In assigning *Victoriacystis* to the Placocystitidae (amended from Placocystidae Caster, 1952), Gill and Caster (1960) postulated that *Placocystites*, *Rhenocystis* and *Victoriacystis* could be arranged in an evolutionary sequence, characterized by an increase in the number of transverse rows of ventral plates. However, examination of better preserved, recently collected material of *Victoriacystis* (Ruta 1997) shows that this genus possesses five rows of ventral plates, and not six as proposed by Gill and Caster (1960).

Ubaghs (1968, p. S555) grouped Anomalocystida and Placocystida into a single suborder Anomalocystitida, because the distinction made by Caster (1952) between these suborders was based on '... the erroneous assumption that the Anomalocystitida [*sic*] are provided with segmented brachia and the Placocystida with unsegmented rodlike processes. In fact, as demonstrated by Caster ..., the Anomalocystitida [*sic*] have no jointed brachia ... Therefore they do not differ in any essential way from the placocystid genera' [the segmented brachia and the rodlike processes correspond to the



TEXT-FIG. 7. Alternative three-taxon/three-area arrangements for the anomalocystitid mitrates *Placocystites forbesianus*, *Rhenocystis latipedunculata* and *Victoriacystis wilkinsi*. A, the results of a parsimony analysis indicate that *Placocystites forbesianus* is the sister group to *Rhenocystis latipedunculata* + *Victoriacystis wilkinsi*; B, a compatibility analysis places *Victoriacystis wilkinsi* as the sister group to the clade (*Placocystites forbesianus* + *Rhenocystis latipedunculata*).

articulated spines in the terminology adopted here]. Ubaghs (1968) placed *Placocystites* and *Rhenocystis* in the family Anomalocystitidae together with *Anomalocystites*, *Ateleocystites* Billings, 1858, *Basslerocystis* Caster, 1952, *Enoploura* and *Victoriacystis* (according to Parsley 1991, *Basslerocystis* is a junior synonym of *Anomalocystites*). Other anomalocystitid genera were assigned to the families Australocystidae Caster, 1954 and Allanicytidiidae Caster and Gill, 1968.

A sister group relationship between *Rhenocystis* and *Victoriacystis* was first proposed by Parsley (1991) in his reconstructed phylogeny of the anomalocystitids, in which the families Anomalocystitidae and Placocystitidae were kept separate. One of us (MR) is currently working on a comprehensive cladistic analysis of the anomalocystitids using the program PAUP version 3.1.1 (Swofford 1993). The analysis, which will form the subject of another paper, yields three equally parsimonious trees in all of which *Placocystites forbesianus* is placed as the sister group of (*Rhenocystis latipedunculata* + *Victoriacystis wilkinsi*). The characters are optimized using the accelerated transformation (ACCTRAN) option of PAUP, whereby homoplasies are accounted for in terms of distal reversals by placing character changes as close to the tree root as possible (Kitching 1992). For the purposes of the present paper, we shall focus on the character distribution in *Placocystites forbesianus*, *Rhenocystis latipedunculata* and *Victoriacystis wilkinsi.*

The clade (*Placocystites forbesianus* + (*Rhenocystis latipedunculata* + *Victoriacystis wilkinsi*)) (Text-fig. 7A) is supported by three characters. The first character, uniquely shared by these three taxa, pertains to the shape of the lateral margins of the left and right dorsal plates PM, which are strongly convex lateralward throughout most of their length. The second character shows one reversal, and refers to the presence of a suture between plates V3 and V12 (observed in *Placocystites* and *Rhenocystis*, but not in *Victoriacystis*). The third character relates to the presence of two short, straight margins which truncate the left and right postero-lateral angles of plate V3 (observed in *Placocystites* and *Rhenocystis* and reversed once in *Victoriacystis*).

The sister group relationship between *Rhenocystis* and *Victoriacystis* is supported by five synapomorphies: dorsal terrace-like ridges confined to the left and right plates PM and PLM only; posterior quarter of the lateral margins of the left and right plates PM turned medianward and intersecting the posterior dorsal margin of the head; anterior styloid blade recumbent; fore tail three times as wide anteriorly as posteriorly and occupying most of the posterior head surface; dorsal fore tail plates much smaller than the ventral fore tail plates.

The following eight characters, not uniquely derived, also support the clade (*Rhenocystis latipedunculata* + *Victoriacystis wilkinsi*): ventro-lateral extensions (lateral head walls) of the dorsal lateral marginal plates about as large as their dorso-median extensions; lateral head walls sloping slightly ventro-laterally; flexible upper lip; centro-dorsal plate C much narrower posteriorly than anteriorly; terrace-like ridges confined to the posterior third of the ventral skeleton only; anterior styloid blade expanded transversely; presence of a sharp, mid-dorsal styloid keel; styloid keel projecting on the dorsal surface of the anterior styloid blade.

DISCUSSION

Rhenocystis differs from *Placocystites* in having five rather than four transverse rows of ventral plates (Dehm 1932, 1934; Caster 1952; Ubaghs 1968), and from *Victoriacystis* in that the ventral plates of the second row are relatively small in comparison with those of the first and third rows (Ruta 1997). In *Placocystites*, the two anteriormost transverse rows of the ventral skeleton correspond to the first and the third row of *Rhenocystis* and *Victoriacystis*. On the basis of its ventral plating pattern, *Placocystites* may be regarded as the end member of an evolutionary lineage in which the second row of central plates (which completely separates the first from the third row in *Victoriacystis*) became progressively reduced in size (as in *Rhenocystis*), and eventually disappeared (the condition observed in *Placocystites*).

The most parsimonious distribution of character changes, however, shows that the reduction of the second row in *Rhenocystis* and its loss in *Placocystites* do not represent successive stages of a transformation series. Interestingly, Gill and Caster (1960) hypothesized that an increase rather than a reduction in the number of ventral plates characterized the anomalocystitids of boreal type. Part of their argument, however, was based on an incorrect reconstruction of the plating pattern of *Victoriacystis*, as explained above (Ruta 1997).

The sister group relationship between *Placocystites* and the two sister taxa *Rhenocystis* and *Victoriacystis* maximizes character congruence, and should be preferred to alternative arrangements emphasizing conjectures of morphological transformation. However, it is interesting to compare the results of the parsimony analysis with those of a compatibility analysis (MR, unpublished data) in which *Victoriacystis wilkinsi* is placed as the sister group of (*Rhenocystis latipedunculata* + *Placocystites forbesianus*) (Text-fig. 7B). Depending upon which of the three equally parsimonious trees obtained with PAUP is considered, the arrangement (*Victoriacystis wilkinsi* + (*Rhenocystis latipedunculata* + *Placocystites forbesianus*)) found in the compatibility run requires eight or nine additional steps in the parsimony analysis.

The sister group relationship between *Rhenocystis* and *Victoriacystis* has interesting implications for the phylogeny and the palaeobiogeography of the anomalocystitids. It has long been assumed that the boreal and the austral taxa formed two distinct groups, but very few studies have attempted to test this hypothesis against a phylogenetic framework (see Derstler 1979). New anatomical information on *Victoriacystis* (Ruta 1997) shows that this mitrate has boreal affinities and it is not closely related to other anomalocystitids from the southern hemisphere, contrary to previous suggestions (e.g. Parsley 1991; Ruta and Theron 1997).

Almost certainly, an active interchange of anomalocystitid faunas between the northern and the southern palaeocontinents must have taken place in the late early or early mid Palaeozoic (Derstler 1979). That an interchange occurred is also confirmed by the recent description of the early Devonian South African mitrate *Bokkeveldia oosthuizeni* (Ruta and Theron 1997), the ventral plating pattern of which closely resembles that of several boreal taxa such as *Anomalocystites* (see Parsley 1991). For Caster (1954) and Derstler (1979), the Siluro-Devonian austral mitrates clearly derived from boreal forms.

A cladistic analysis (MR, unpublished data) shows that the vast majority of austral anomalocystitids, represented by the family Allanicytidiidae (Caster and Gill 1968; Philip 1981; Caster 1983; Haude 1995; Ruta and Theron 1997), is closely related to the mid to late Ordovician North American genus *Enoploura*. *Rhenocystis* and *Victoriacystis*, on the other hand, constitute the most derived taxa within a clade consisting mainly of boreal forms. The history of this clade is still poorly understood.

Unpublished data (MR) on ancestral area reconstructions applied to the Anomalocystitida as defined by Ubaghs (1968), as well as to several subgroups within this clade, indicate that North

America is the most likely to be part of the geographical area in which the anomalocystitids of boreal type (including *Rhenocystis*) originated. The ancestral area data were obtained using the approach devised by Bremer (1992, 1995; see also Ronquist 1994, 1995 for a discussion). Briefly, the Bremer method assesses the probability that the geographical area in which a taxon is found is also part of the ancestral distribution of the group to which that taxon belongs. Each area character is optimized according to two complementary approaches. First, the assumption is made that area absences represent the derived state. Second, it is assumed that area presences are the derived condition.

It is possible to hypothesize that the Anomalocystitida migrated several times from the boreal to the austral continents between the late Ordovician and the Early Devonian, and that North America represented the centre of origin of the group (see also Derstler 1979). Allanicytidiidae (Caster and Gill 1968) perhaps constitutes the only anomalocystitid clade whose origin and evolutionary history were entirely confined to the southern hemisphere.

However, such model is highly speculative and relies on contingent evidence from the poor fossil record of the group; the possibility that the anomalocystitids had a wider geographical distribution and that their centre of origin lay outside North America cannot be ruled out.

CONCLUSIONS

The number of anomalocystitids described during the last 30 years equals that known at the time of publication of the *Treatise on invertebrate paleontology* (Ubaghs 1968). It took more than a century to recognize these fossils as a distinctive group after the first published account of a representative of them (Billings 1858). Several recent studies have provided insights into their detailed morphology and character distribution (e.g. Jefferies and Lewis 1978; Kolata and Guensburg 1979; Parsley 1991; Haude 1995; Ruta 1997), and new material awaits proper description (Derstler 1979).

In this paper, *Rhenocystis latipedunculata* Dehm, 1932 from the German Lower Devonian is redescribed and its relationships are discussed. The general morphology and plate arrangement of *Rhenocystis* fit into the anatomical pattern of the boreal taxa from which, however, *Rhenocystis* differs in several respects. *Rhenocystis* most closely resembles *Victoriacystis* and *Placocystites*, and represents an important link between austral and boreal Siluro-Devonian mitrates.

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